Title: Fear and foraging interact with temperature and seasonality to drive diversity in fish life histories

Running Title: Ecosystem size spectra drive life history diversity

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Abstract

Understanding how fish growth and reproduction will adapt to changing environmental conditions is a fundamental question in evolutionary ecology, but predicting the responses of specific taxa is challenging. Analyses of the physiological effects of climate change upon life histories and population demography rarely consider size-dependent foraging and risk of predation. We embedded a state-dependent energetic model in an ecosystem size spectrum to model prey availability (foraging) and risk of predation (fear) experienced by individual fish as they grow. We found that asymptotic growth emerged from size-based foraging and reproductive and mortality patterns in the context of ecosystem food web interactions, without *a priori* assumptions about the onset of reproduction. While more productive ecosystems led to larger maximum body sizes, the effects of temperature on body size were surprisingly small. To validate our model, we ran it for abiotic scenarios corresponding to the three ecological lifestyles of tunas, considering environments that included seasonal variation in temperature. We successfully predicted realistic patterns of growth, reproduction, and mortality of all three tuna species with distinct ecological lifestyles. Unexpectedly, we found that individuals grew larger when they experienced higher productivity or colder temperatures for part of the year, due to seasonal migrations. This increase in body size emerged because spawning opportunities were seasonally constrained, and explains the evolution of gigantism in temperate tunas. Our approach combines direct and indirect effects of productivity (foodscapes) and individual risk (fearscapes) with metabolic processes and offers a promising approach to understand fish life-history responses to changing ocean conditions.

Introduction

The body sizes and population biomasses of aquatic species are changing rapidly to human-induced environmental change (Oke et al. 2020), motivating the need for mechanistic models to predict growth and reproduction in response to changing environmental conditions (Cheung et al. 2008, Cheung et al. 2010, Blanchard et al. 2012, Fernandes et al. 2020). Beyond thermal physiology, the evolutionary consequences resulting from changing ecosystem productivity (foodscapes) and predator abundance (fearscapes) are difficult to disentangle from the effects of changes in prey abundance, predation risk or seasonality on growth and related life history traits (Daufresne et al. 2009, Audzijonyte and Richards 2018, Neubauer and Andersen 2019). Classic and recent advances predicting optimal growth and reproduction of harvested populations (Holt 1958; Beverton and Holt 1959; White et al. 2022) have been combined with size-structured community interactions to predict the evolution of life history traits in specific taxa (Shuter et al. 2016). This approach provides a promising foundation for predicting ecological and evolutionary responses to environmental and climate change. While specific taxa within an ecosystem will adapt according to contextual factors such as phylogenetic lineage, adaptive capacity, and environmental variability, mechanistic models incorporating the roles of foodscapes and fearscapes, seasonality, and other metabolic processes could explain adaptive variation among closely related taxa and refine our mechanistic understanding of species' responses to changing environmental and climate conditions (Free et al. 2019). By examining closely related tuna species (Scombridae) that have invaded different environmental niches, we can gain insight into how physiological adaptations to thermal conditions, productivity and their seasonality affect allocation to growth and reproduction. This can help move us beyond broad macro-ecological

patterns toward a more mechanistic understanding of the drivers of existing diversity and improve predictions of species-specific responses to future change (Alvarez-Noriega et a. 2023).

In ectothermic species with indeterminate growth, including fish, food availability and risk of predation both increase as individuals grow larger, and growth rates can be selected to be slower or faster depending on the size-dependence of per-capita resource availability and predication risk (Conover and Munch 2002; Walsh and Reznick 2009, Hulthén et al 2021). At the same time, development at higher temperatures can lead to smaller body sizes, within and between ectothermic species (Kingsolver and Huey 2008). Trade-offs among these life-history traits determine individual body sizes and population demographic rates (Beverton and Holt 1959, Gadgil and Bossert 1970, Kozlowski 1992, Kozlowski 1996), but existing theory struggles to predict how size-dependent changes in prey availability and decreases in predation risk, along with interacting effects of temperature and seasonality, affect the evolution of growth (Varpe 2017). There is longstanding interest in understanding the mechanisms leading to biphasic or asymptotic growth patterns (Quince et al. 2008). The earliest growth models, including the von Bertalanffy growth model, were based on hypothesized differences in the allometric scaling of anabolism (resources taken in) and catabolism (resources spent) (von Bertalanffy 1960, Audzijonyte et al. 2022). Such growth models are routinely fit to data on size-at-age of fishes, but their mechanistic justification is necessarily simplistic; such models struggle to explain spatial and temporal trends in body size within and among species of fish (Audzijonyte et al. 2020), suggesting that they do not sufficiently capture the relevant intrinsic physiological and extrinsic ecological drivers of fish life histories.

The role of metabolic requirements and the trade-off between growth and reproduction in shaping growth trajectories has been given increasing attention in recent decades (Jørgensen et al. 2016, Wong et al. 2021, White et al 2022). Physiological processes can vary with the environmental temperature experienced by organisms (Brown et al, 2004, Clarke and Johnston, 1999). The allometric scaling of metabolic costs in different temperature regimes (known as the Metabolic Theory of Ecology [MTE]; Gillooly et al. 2001) has been used to predict individual body size according to the benefits of growing large (to increase foraging success and avoid predation), balanced against the costs of increased metabolic overhead and diverting resources from reproduction to growth (Wong et al. 2021). More detailed dynamic models of energetic allocation have linked variable environmental conditions to growth, reproduction, and longevity (Kozłowski and Teriokhin 1999, Cichoń and Kozłowski, 2000, Lika and Kooijman 2003, Jorgensen and Fiksen 2006, Audzijonyte et al. 2022). Understandably, the results of these energetic budget models depend on specific assumptions regarding mass-based foraging success and risk of predation. Generalizing these prior results requires a unified framework incorporating metabolic demands, access to resources, and predation risk in environments of differing temperatures, productivity, and seasonality.

We draw on ecosystem size-spectra theory to reduce the number of *ad hoc* assumptions required about the scaling of ecological processes - foodscapes and fearscapes - that arise from community interactions. We hypothesize this approach could yield more realistic predictions of diversity in fish life histories, providing significant insights into the mechanisms that determine adaptive responses to changing environmental conditions. In aquatic ecosystems, size spectra are an emergent property of community interactions (Sheldon et al. 1977, Thygesen et al. 2005, Law

et al. 2009, Sprules and Barth 2016, Christensen and Andersen 2011, Andersen et al. 2016, Andersen 2019). In a community size spectrum, flow of energy between trophic levels via consumption and predation rates are characterized by individual mass, instead of species' identity (Benoît and Rochet 2004, Blanchard et al. 2009, Andersen 2019). The key property of size spectra is that an individual's relative position (mass) determines both its prey field (foodscape – or the area under the size spectrum to the left of an individual's mass) and its risk of predation (fearscape – the area to the right). Individuals are born small and grow through the size spectrum over their lifetime, consuming prey that are a fraction of their own size. Furthermore, size-spectrum theory assumes the lower limit of prey size preference depends on the profitability of the prey, and any upper limit depends on the maximum gape size of the predator. These interactions could equally apply to interactions within size-structured populations of the same species (i.e., cannibalism). Therefore, predation and consumption rates determined by different areas under a size-spectrum curve could be used to simultaneously characterize the mass-specific caloric resource availability and risk of predation experienced by an individual as it grows (Benoît and Rochet 2004, Giacomini et al. 2013, Shuter et al. 2016, Andersen 2019).

Here, we used an energetic model combining size-dependent resources and risk of predation (both derived from size-spectra) with size- and temperature-dependent physiological requirements to predict the evolution of diverse fish life histories including growth, maximum body size, reproductive investment, and longevity in different environments. We defined fitness as expected lifetime reproductive success and determined its maximum value and the associated life history decisions (allocation to maintenance, growth and reproduction) using stochastic

dynamic programming (Clark and Mangel, 2000, Houston et al.1988, Mangel, 2015). We used this approach to examine general patterns in the life history evolution of fishes under different scenarios of ecosystem productivity and environmental temperature.

We next investigated the evolution of growth, body sizes and reproductive patterns in tuna species under several environmental scenarios with varying temperatures, ecosystem productivities and seasonally varying conditions. Tunas (Family Scombridae) exhibit a wide range of maximum body sizes (~ 40 cm - 400 cm), longevities (~ 4 - 41 years) and reproductive patterns (Juan-Jorda et al. 2013, Horswill et al. 2019). Tunas are epipelagic species found in temperate and tropical waters around the world's oceans with varying vertical, latitudinal and seasonal distributions and movements. Confronting the predictions of our general model with data on the life history diversity observed in tuna species in different environmental conditions provided insight into the mechanisms underlying fish life histories. Where possible, our models were parameterized with values for physiological processes measured for tunas, but we also considered the sensitivity of our results to these parameters to ensure their generality across the diverse life histories observed in fishes.

Methods

We used size-spectrum theory to infer mass-specific rates of prey encounter and mass-specific rates of predation. The relationship between the numbers of organisms and individual mass w is a power function with a scaling parameter κ and an exponent λ, which has been empirically estimated to be close to -1 such that abundance is inversely proportional to mass (Sheldon et al. 1972, Trebilco et al. 2013, Sprules and Barth 2016, Hatton et al. 2021)

$$N(w) = \kappa w^{\lambda} \quad (1)$$

The Sheldon size spectrum, which follows from Eq. 1, is the distribution of total ecosystem biomass *B(w)* across body size classes, and is represented by $B(w) = N(w)w$. Based on evidence from multiple ecosystems (Sprules and Barth 2016), the spectrum – as originally conceived (Sheldon et al 1972) and recently confirmed (Hatton et al. 2021) – is nearly flat, or may very slowly decrease as body size increases. Since $N(1) = \kappa$, we view κ as a metric of ecosystem productivity. In a log-log plot of Eq. 1, the intercept is the log(κ).

This phenomenon of linear aquatic size spectra emerges from three size-dependent processes: (1) the encounter rate of predators and prey; (2) the preference of predators for prey of a given size; and (3) the limit to prey consumption imposed by the size of the predator's stomach (the predator-prey mass ratio; Benoît and Rochet 2004, Blanchard et al. 2017, Andersen 2019). Anderson (2019) derived a method to calculate the prey available to individuals of mass *w* by relating the productivity of a spectrum to empirical estimates of prey encounter rates, predator-prey mass ratios, and prey preferences. Following his rationale, we assumed that the prey biomass available to an individual is a concave function of mass *w*, and scaled to be approximately three times the size spectrum productivity κ (Andersen 2019). The empirical estimates of physiological processes used to simplify this derivation are associated with a significant amount of variability among species within a size class (Andersen 2019). Following Andersen, as a baseline the per-period food available for an individual of mass *w* is represented by

$$B_{prey}(w) = 3\kappa w^{0.05} \quad (2)$$

This equation approximates the integral over the foodscape of prey biomass (in kg) available to an individual of mass *w* each month (Fig. 1A), and includes a threefold scaling factor from empirical analyses (Andersen 2019). The foodscape is therefore the total biomass available to the predator, and the range of sizes of prey that it takes. To address variability across ecosystems in productivity, we chose to vary κ in subsequent analyses, representing potential differences among taxa or other ecosystem processes.

Second, to infer mass-specific risk of predation, we defined the fearscape as an individuals' instantaneous risk of predation, integrated across sizes of potential predators. For gape-limited taxa like fishes, a predator's prey field depends on its encounter rate with prey in its preferred size range. This encounter rate (the clearance rate) is typically measured in units of volume per time, as aquatic species forage in a three-dimensional habitat (Kiørboe and Hirst 2014). Again, we followed Andersen (2019), and in Eq. 3 (defined below) we used an empirically estimated constant of 0.07 to characterize the scaling of prey vulnerability with its mass, which is based on estimates of preference windows of predators and the volume of water each clears per month that come from empirical distributions of prey sizes in predator guts (Ursin 1973). We also define a coefficient *h,* which modifies the probability of consumption - how likely a predator is to capture the focal individual (based on its hunger level or capture efficiency) - and used the reported allometric exponent of -0.25 to represent how predation mortality scales with body size (Figure 1B; Eq. 2.22 in Andersen 2019). From these, Anderson (2019) integrated over the Sheldon

spectrum to produce a relationship predicting the scaling of mortality risk for prey $\mu_p(w)$ per month:

$$\mu_p(w) = 0.07hw^{-0.25} \tag{3}$$

We convert this instantaneous rate to the probability of escaping from predators during each time interval (Hilborn and Mangel 1997, Mangel 2006), so we can represent the probability an individual survives $\gamma_{pred}(w)$ as:

$$\gamma_{pred}(w) = e^{-\mu_p(w)} \tag{4}$$

The resulting mass-specific survival through each month is plotted for different values of h in Fig. 1B.

Defining physiological costs that depend on temperature and body mass

Our energetic model includes physiological costs which depend on temperature and body mass. We assumed that metabolic costs increase with body mass and environmental temperature (Clarke 2006). We modeedl individual costs $C(w,\tau)$ (in joules) as a function of temperature τ in Kelvin, following the general form introduced in the MTE (Gillooly et al. 2001):

$$C(w,\tau) = cw^{\theta}e^{\left(-E/k_B\tau\right)} \tag{5}$$

Evidence for the MTE suggests the activation energy E (the energy required for the reactions of respiration and other metabolic processes) does not vary appreciably among taxa (Bernhardt et al. 2018); Boltzmann's constant k_B also does not vary. The normalization coefficient c accounts for differences among taxonomic groups in the intercepts of the linear relationship that arise from second-order effects such as stoichiometry or respiratory surface areas (Bigman et al 2021). The slope of this relationship in log space, θ, is strikingly similar among taxa (Brown et al. 2004). We used a value for θ estimated from physiological studies on tunas (Table 1) but varied it in sensitivity analyses. Note that τ in Eq. 5 is traditionally in Kelvin. However, we rescale all values in our results in units of Celsius. We use this general formula for scaling of metabolic costs at different temperatures τ to describe the monthly energetic expenses of an individual of mass w (Fig 1C). Defining the relationships in Eqs. 2, 4, and 5 allowed us to specify mass-dependent survival and energy dynamics and therefore examine the variables influencing growth and reproduction in a common currency of individual fitness. All parameters are defined and their values reported in Table 1.

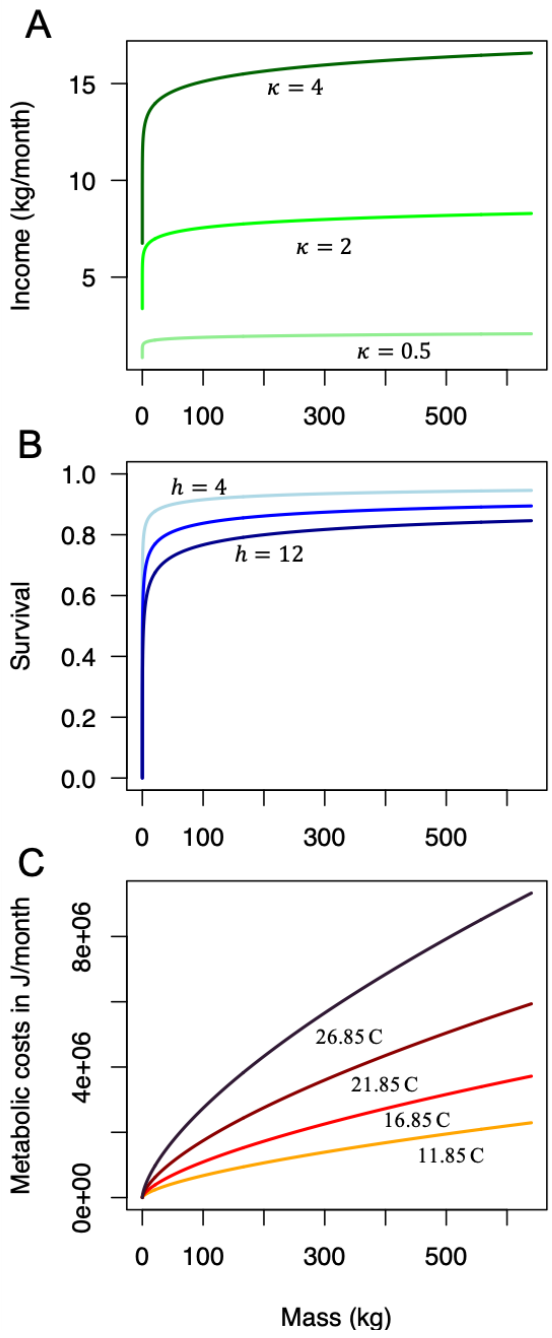

Figure 1. Examples of allometric relationships between individual mass and (A) income (in kg per month) for differing ecosystem productivities κ (Eq. 2); (B) the scaling of survival with size and its interaction with predator efficiency (or hunger) h (Eq. 4), such that higher values of h represent more efficient predators; and (C) metabolic costs (Eq. 5), which also scale with temperature τ (on the graph, it is presented in degrees Celsius, °C; values in Kelvin are 285, 290, 295 and 300K). Note that these curves represent a subset of values considered in our results.

Defining fitness and determining the optimal allocation strategy

To find the optimal life history strategy in different scenarios of ecosystem productivity and temperature conditions, including seasonal variation in the scenarios, we developed a model of an individual's energy budget, tracking two physiological state variables, the body length l and energy (lipid) stores s of an individual, which vary dynamically over an individual's lifetime (Fig. 2). Following the conventions for dynamic state-variable models, we denoted the state variables l and s are lowercase in the dynamic programming equation, representing the fact they are iterated values; potential future states are denoted as l' and s'. Later, when we refer to specific values of the state variables, we use uppercase L and S.

We define fitness as expected lifetime reproduction, averaged over the stochastic process of survival, which we calculated numerically using stochastic dynamic programming (Houston et al. 1988; Clark and Mangel 2000, Mangel, 2015). This method allowed us to consider how individual age and physiological state (energy stores and body length) affect the optimal trade-off between growth and reproduction in the context of lifetime fitness. We assumed that an individual allocates a proportion of its budget to growth and reproduction on monthly time intervals. Our choice to model allocation to growth and reproduction as proportions of an individual's energy budget builds on prior dynamic state-variable models of fish growth (Jørgensen and Fiksen 2006, Chapman et al. 2011).

Given specific values of $L(t)$ and $S(t)$, representing individual length and energy stores at the start of month t, structural mass $W(t)$ is related to length with a standard cubic function (Froese 2006):

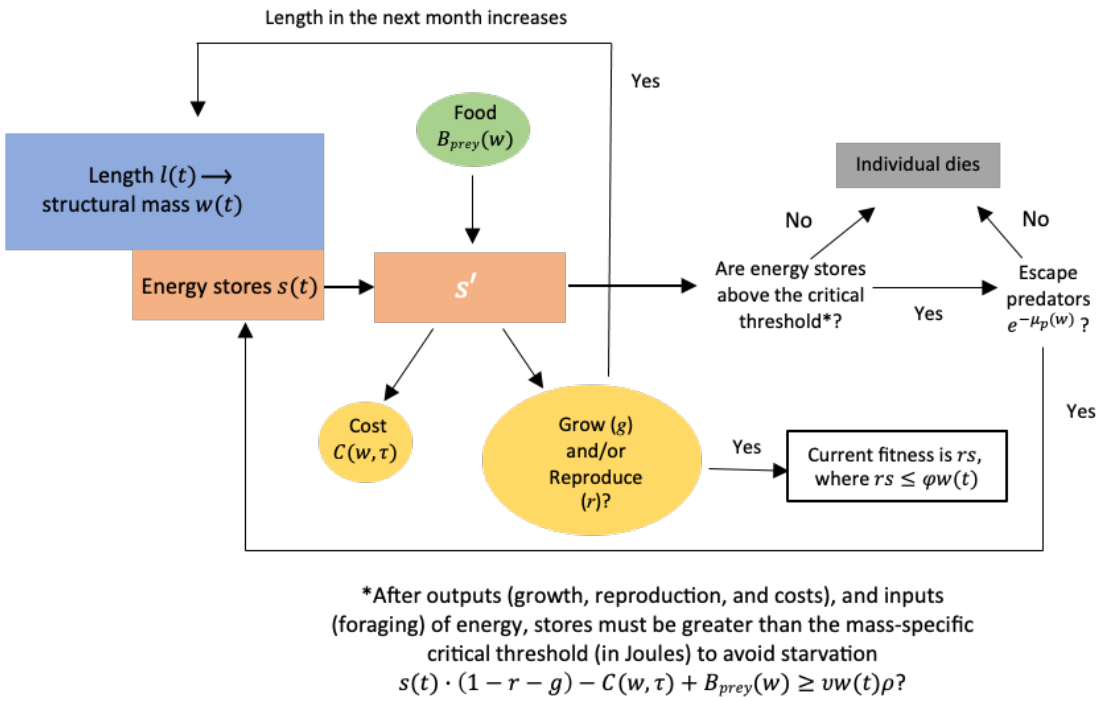

Figure 2. Conceptual overview of the optimization algorithm calculating the two dynamically varying state variables, body length $l(t)$ and energy stores $s(t)$ within each month t, as well as current and expected fitness. Arrows represent the flow of energy or decisions. Round shapes represent energetic input (green) and outputs (yellow); rectangular shapes are model states and outputs (fitness and fate). Note that $l(t)$ and $w(t)$ are related through Eq. 6. Both B_{prey} and μ_p are determined by the size spectrum.

$$W(t) = aL(t)^3 \tag{6}$$

We assumed that only structural mass is relevant for size-dependent gains (B_{prey}) and costs (C) (Fig. 2). We convert from mass to units of energy (joules) and back using a conversion factor

estimated for tunas ($\rho = 4.2 \times 10^6$J/kg; Chapman et al 2011) but that could take other values for other species. Each month, an individual acquires energy from food, determined by their structural mass *w* via Eq. 2. We then allowed the individual to allocate proportions of its energy budget (which includes income and any stored energy) to growth (*g*) and reproduction (*r*). Given an individual with specific values for length $L(t)$ and energy stores $S(t)$, we calculated the increment of growth expected for each possible proportional allocation *g* by converting the fraction of lipid stores from joules to the equivalent mass ($g\frac{S(t)}{\rho}$), and then adding it to existing mass, such that $W(t+1) = W(t) + g\frac{S(t)}{\rho}$. We then calculated the new length by rearranging the mass-length relationship $W(t) = aL(t)^3$:

$$L(t+1) = \left(L(t)^3 + g\frac{S(t)}{a\rho}\right)^{1/3} \tag{7}$$

We repeated this for every possible combination of values of the state variables, *l* and *s*. Values for proportional allocation of lipid stores to reproduction *r,* along with *g,* combine to determine the dynamics of energy stores and length from one month to the next:

$$S(t+1) = B_{prey}(W(t)) - C(W(t),\tau) - (r+g)\cdot S(t) \tag{8}$$

We assumed that both stored energy and reproduction were limited by an individual's structural mass (which in turn depends on its length). These constraints represent limits on both the amount of lipid can be stored, and the mass of gametes that can be produced, given the capacity of the body cavity. If the proportions of energy allocated to reproduction and growth were less than 100% (meaning $r + g < 1$), the remaining energy was assumed to be stored for future use, given

that total reserves did not exceed 60% of structural mass. This value was arbitrary, but exploratory analyses suggest it did not have a strong effect on the results presented here because in practice individuals do not store their energy long enough to come close to exceeding this limit. Reproductive output (in units of kg) was similarly constrained so that it cannot exceed a fixed proportion of φ of structural mass $w(t)$, such that the following condition must be met:

$$\frac{rS(t)}{\rho} \leq \varphi w(l,t) \tag{9}$$

This size-based limit on total reproduction is used in the calculation of current fitness.

Expected future fitness

At any age, expected fitness was the sum of current reproduction and accumulated future reproduction, which was calculated assuming the individual behaved optimally for all future ages. This required calculation of the future states (length and lipid stores) given each combination of allocation to growth and reproduction. We denoted potential values of future states as $l'$and s'. These are

$$l'(l,s,g) = l + \left(l(t)^3 + g\frac{s}{a\rho}\right)^{1/3}$$

$$s'(l,s,r,g) = B_{prey}\big(w(l)\big) - C(\,w(l),\tau) - (r+g)s \tag{10}$$

where $w(l)$ is the structural mass of an individual of length *l.* At the end of the month, if an individual's lipid stores fell below the critical threshold for its mass (its expenditures have

exceeded its energy budget), it starved (Supp. Fig. 2). We let $\gamma_s(s,l)$ denote the probability of avoiding starvation in the current time and modeled it as

$$\gamma_s(s,l) = \frac{1}{1+e^{-q(s-\upsilon w(l)\rho)}} \tag{11}$$

involving two new parameters υ and q. The parameter υ determined the level of stores at which starvation begins; q is a shape parameter. When $s = \upsilon w(l)\rho$, the right-hand side of Eq. 11 is always ½. When q is large, then the right-hand side of Eq. 11 is approximately one when $s > \upsilon w(l)\rho$ and zero otherwise. Thus, this function specified that if combined allocation to growth and reproduction caused an individual's lipid stores to decrease below the critical value for its mass, its probability of survival decreased smoothly toward zero (See Supp. Fig. 1 for more details).

Equations 7-11 characterize changes in individual state and in fitness, given all possible monthly allocation strategies (r and s). With these functions in place, we can find the allocation strategy that maximize current and future fitness at every age until the age of senescence or maximum lifespan, T, is reached (for all scenarios, we assumed the maximum lifespan of T = 216 months or 18 years). We define $V(l,s,t)$ as the maximum expected accumulated reproduction between time t and T, given size $L(t) = l$ and lipid stores $S(t) = s$. Since there can be no accumulated reproduction after T, we assumed $V(l,s,T) = 0$. Expected future fitness at every age $t < T$ was found by solving the stochastic dynamic programming equation

$$V(l,s,t+1) = \max_{g,r}\left[R(r,l,s,t) + \gamma_{pred}(w)\cdot\gamma_s(s,l)\cdot V\big((l'(l,s,g), s'(l,s,r,g), t\big)\right] \tag{12}$$

The first term of the on the right-hand side of Eq. 12 represents reproduction in month *t*. The second term represents expected future reproduction, discounted by the probability of surviving predation $\gamma_{pred}\ (w)$ and starvation $\gamma_s(s, l)$, When these are combined, we can obtain expected lifetime reproduction from time *t* onwards, given that size $L(t)\ =\ l$ and lipid stores $S(t)\ =\ s$.

The dynamic programming algorithm (Mangel and Clark 1988; Houston and MacNamara 1999) iterates over all viable combinations of *l* and *s,* at each time *t,* and stores the fitness of each allocation strategy. The optimal strategy (marked with an asterisk) at time *t* is the combination $g*$ and $r*$ associated with the greatest current and future fitness. Further details of the optimization algorithm are given in the Appendix. In Supp. Fig 3 we illustrate the array for both allocation strategies (*g*(l,s,t)* and *r*(l,s,t)*) at two ages, for all possible combinations of length and lipid stores.

Calculating the fate of individuals allocating optimally

We used a Monte Carlo simulation to calculate the accumulating probability of mortality as an individual ages, following the allocation rules generated by the solution of Eq. 12, which provides optimal allocation rules for the range of state values specified in our numerical algorithm. Some combinations of states (length, lipid stores and age) will not arise naturally and others are inviable (the dark blue regions of Supp. Fig. 3). Therefore, to predict the relationships between length, lipid stores, and age that will be observed in nature, we simulated the expected fates of an individual that is born at a given size, and allocates energy according to the optimal growth and reproduction fractions given by the solution to Eq. 12. We recorded the body length

373 and reproductive output in each subsequent month of an individual's life, and calculated its
374 probability of survival, given both the risk of starvation and the risk of predation. The expected
375 lifespan was defined as the age past which the cumulative chance of survival is less than 3%,
376 which we used as an arbitrary definition of lifespan. For simplicity, we considered reproductive
377 output in units of energy (joules) rather than considering allocation to offspring size and number
378 (Kindsvater et al. 2010); this can include migration costs. We did not build in any assumptions
379 about age at maturation, but rather let maturation patterns, along with natural trade-offs between
380 growth and reproduction (Supp. Fig. 3) emerge from patterns of allocation.
381
382 *Scenarios for environmental variation*
383 We used our general energetic model to predict a range of fish life histories (growth,
384 reproduction, and survival) that are evolutionarily advantageous across different scenarios of
385 ecosystem productivity and environmental temperatures. To do this, we developed different
386 productivity and temperature scenarios corresponding to different conditions commonly found in
387 the marine environment and impose different metabolic costs to individuals according to Eq. 5.
388 We solved for the optimal life histories under different temperatures (τ in Eq. 5 in units of
389 Kelvin), converted to Celsius and ranging from 11.85 to 26.85 ℃ (285-300 K) in five-degree
390 intervals. We considered these temperature ranges in different scenarios for ecosystem
391 productivity, for which κ ranged from 0.25 to five. We considered factorial combinations of
392 these parameters to understand the implications of their interactions for the evolution of fish life
393 histories.
394
395 *Case study predicting life history diversity of tunas (Scombridae).*

We developed a case study for tunas to examine if our general energetic model predicted the general patterns of life history variation observed in this group of species adapted to different environmental niches. There are 15 species of tunas within the Family Scombridae, from five genera: *Allothunnus*, *Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus* (Collette et al. 2001). These species inhabit a wide range of environmental conditions in marine ecosystems. Paleo-oceanographic evidence suggests that ancestral tunas evolved in a tropical environment approximately 60 million years ago (Monsch 2000) and over time they have diversified and evolved a suite of morphological and physiological adaptations that have allowed them to expand their distributions into more temperate environments or deeper colder waters where they can encounter higher prey densities to support their high somatic and gonadal growth rates (Dickson and Graham 2004). Currently, tunas can be found in coastal and oceanic pelagic waters, and have wide geographic distributions, ranging from the tropics to higher temperate latitudes with some degree of habitat partitioning by depth. Tropical tunas can spawn throughout the year, while the subtropical and temperate tunas undergo seasonal migrations returning form cool high latitude feeding grounds back to warm waters for spawning (Juan-Jordá et al 2013, Horswill et al 2019). Reflecting their tropical ancestor, all tunas (except for the slender tuna *Allothunnus fallai*) spawn in warm waters, requiring a sea surface temperature of at least 24 ℃ (Schaefer 2001). This is a key aspect of their reproductive biology that we include in our model scenarios.

To connect our general energetic model more explicitly with the observed patterns of life history variation in tunas, we followed a proposed categorization of tunas into three ecological lifestyles (Bernal et al. 2017). The three general lifestyles are based on species-specific vertical,

latitudinal, and temporal (seasonal) distributions and movement patterns of tunas (Figure 3; Bernal et al. 2009, Bernal 2011, Bernal et al. 2017). The first ecological lifestyle represents a tuna species that largely remains within the warmer and well-oxygenated surface layer above the thermocline (generally above 20 °C) during both day and night. These tuna species have limited vertical movements as they do not descend below the thermocline (Figure 3). Coastal species, such as the tropical frigate tuna (*Auxis thazard*) may typify this group. The second ecological lifestyle represents tuna species that spend the majority of the time above the thermocline (generally above 20 °C) but also visit depths below the thermocline for foraging (Figure 4). The oceanic species of yellowfin tuna (*Thunnus albacares*) with year-round tropical distributions typifies this group. Its vertical movement exposes this species to a wider range of temperatures and to less-oxygenated waters at depth but only for short periods of time because this species is not hypoxia tolerant (Schaefer et al. 2009). The third ecological lifestyle characterizes tuna species that are exposed to a wider range of environmental conditions and spend significant periods of time in colder waters (Figure 3). The oceanic and temperate Atlantic bluefin tuna

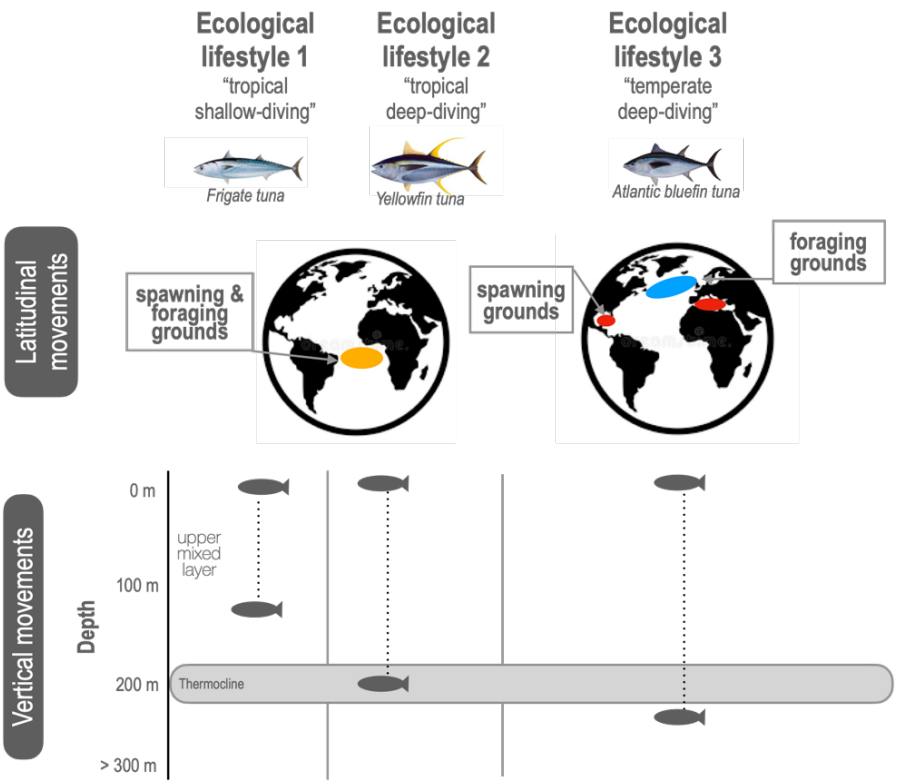

Figure 3. Three representative ecological lifestyles of tunas and their distribution patterns based on their latitudinal and vertical movements. Characteristic spawning and foraging grounds are shown for each lifestyle; The three ecological lifestyles illustrate a tropical shallow-diving frigate tuna *Auxis thazard*, a tropical deep-diving yellowfin tuna *Thunnus albacares,* and a temperate deep-diving Atlantic bluefin tuna *Thunnus thynnus*. Fish silhouettes represent the depth distribution where species spend most of their time. The thermocline is defined as the depth range within which the water temperature changes rapidly and separates the water column into the upper well-mixed surface layer (water above 20 °C) and the deeper waters (waters below 15 °C). Figure modified from Bernal et al. 2009 and Bernal et al 2017.

(*Thunnus thynnus*) are one species that typifies this group, spending most of the year at higher

435 latitudes in colder and more productive waters between the upper mixed later and the cooler deep
436 waters below the thermocline, and migrating to warmer waters for spawning (Bernal et al. 2017).
437
438 To examine whether our general model could predict these three broad ecological lifestyles of
439 tunas, we modelled environmental scenarios corresponding to each lifestyle in terms of
440 temperature, ecosystem productivity, and seasonality (Table 2). We chose parameters based on
441 the results of our general model, but also added seasonal fluctuations in temperature to represent
442 the bluefin tuna migration from temperate, productive waters to their tropical spawning grounds.
443 We then asked whether the life-history traits emerging in these scenarios matched the range of
444 reported sizes of three representative species corresponding to each lifestyle (Juan-Jordá et al.
445 2016).
446
447 *Sensitivity analyses*
448 We ran a series of tests to examine how our choices of parameters in the size spectrum influence
449 model predictions. Specifically, we varied values of h (representing efficiency in prey capture or
450 hunger levels) in the predation function (Eq. 3) and φ (the fraction of body mass that can be
451 devoted to reproduction) in the reproductive constraint (Eq. 9). We also conducted sensitivity
452 analyses in which we varied the scale and shape coefficients in the metabolic cost function (c and
453 θ, respectively, in Eq. 5). Motivated by our tuna case study, we also varied seasonality in
454 resources, temperature, and spawning. We considered seasonal environments in which only
455 resources and only temperature varied, to understand how these factors alone contributed to
456 observed variation in body size and reproductive output. We additionally considered growth and
457 reproductive patterns with an extended warm season (where individuals could spawn in warm

temperatures for six months of the year, instead of three). Finally, we determined in preliminary analyses that the maximum lifespan T did not strongly affect model results, because most individuals reach a maximum body size well before the final time T.

Results

An asymptotic growth pattern naturally emerged from the model, after a period of exponential growth early in life (Fig. 4). Our model predicted age-specific relationships between body size (length, from which we calculate mass using Eq. 6) and reproduction that correspond to a range of fish life histories (Fig 4). In general, we found that individuals allocated energy to growth early in life and shifted this allocation to reproduction in later life. Ecosystem productivity (κ) alone generated a range of maximum body sizes, from less than 100 cm at low levels of productivity to well over 350 cm (Fig. 4A). Across scenarios of ecosystem productivity, the predicted trajectories for individual growth were identical in early life (before age 2); subsequent growth slowed earlier in lower productivity environments (Fig. 4A). For all life histories, allocation to reproduction began at very low levels sometime during the individual's second year (Fig. 4B) and increased steadily as the individual aged. Both the rate at which reproduction increased with size and the maximum reproductive output were consistently greater with increased ecosystem productivity (Fig. 4B). We also found the pattern of age-specific mortality was very similar in early life for all productivities κ, but that lifespan increased predictably as asymptotic body size increased (Supp. Fig. 5).

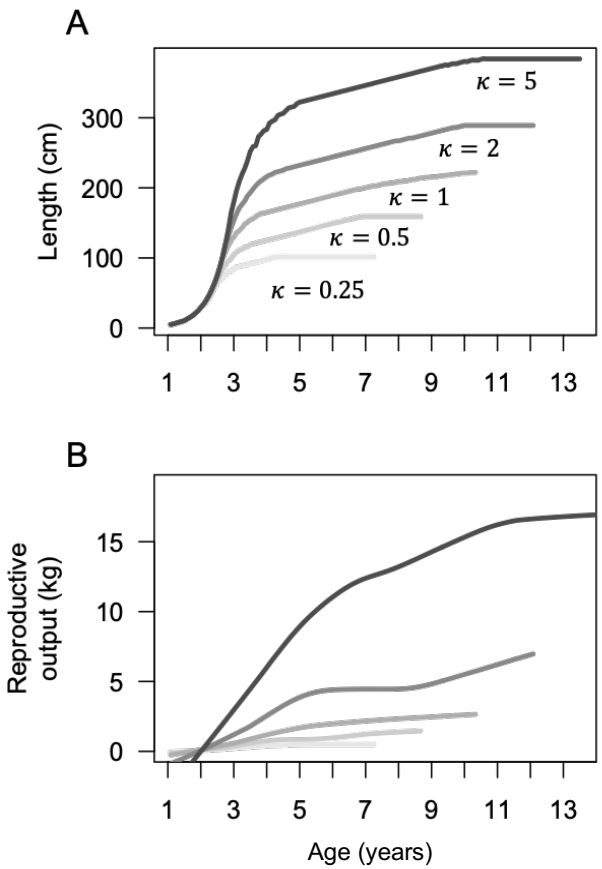

Figure 4. (A) Growth (length at age) and (B) Expected reproductive output of individuals in different productivity κ scenarios. Each curve ends when an individual's expected survival chances are less than 3%. Temperature in every scenario was constant at 16.85 ℃, and h was constant at 8. The reproductive output was smoothed using the loess tool in R; data points can be found in Supp. Fig. 4.

When we compared the interacting effects of ecosystem productivity (κ) and environmental temperature (τ) on patterns of growth and reproductive allocation, we found the effects of temperature on body size and reproductive output were relatively small (Fig. 5). The biggest differences emerged in highly productive environments with dramatic increases in temperature. Specifically, when average temperature increased by 10 degrees (e.g., from 11.85 to 21.85 ℃ or from 16.85 to 26.85 ℃), maximum body sizes were 3-10% smaller, with the largest differences occurring when $\kappa = 5$ (specific values in Fig. 5 are reported in Supp. Table 1). At the same time, these increases in temperature led to concomitant reductions in lifetime reproductive output that ranged from 3-10% (Fig 5B). However, it is important to note that comparing thermal increases

in 5-degree intervals only generated minor (3-5%) decreases in growth and reproduction, unless both predators and prey were scarce ($\kappa \leq 0.5$, Supp. Table 1).

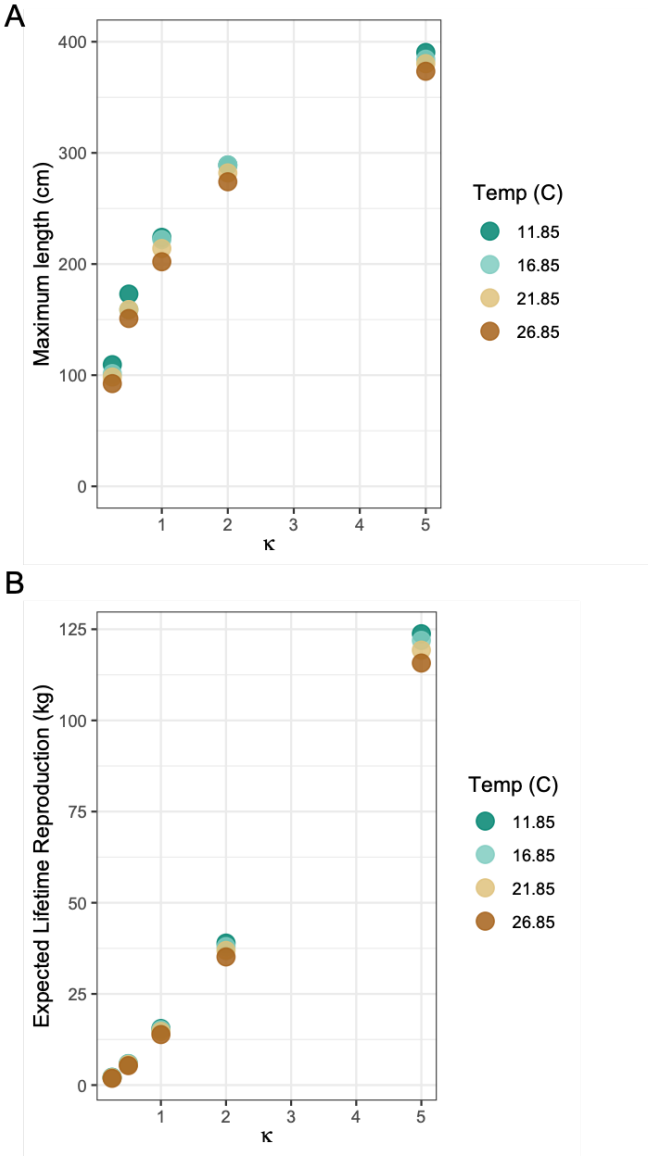

Figure 5. (A) Maximum body size and (B) Expected lifetime reproductive output (in kg) of individuals plotted against a range of productivity scenarios. Color of points corresponds to differences in average annual temperature in °C.

The interacting effects of temperature and productivity on body size showed that when both prey and predators were abundant, the benefits of growing large outweighed associated increases in metabolic costs. Remaining smaller in thermally taxing conditions (to minimize energetic requirements for maintenance), equated to an increased risk of predation and thus shorter

lifespans. In other words, the effect of temperature on survival was indirectly expressed through body size, i.e., where temperature influenced asymptotic body size (Fig. 5A), it had a predictable effect on lifespan.

To understand the robustness of the main results in Figs. 4 and 5, we conducted sensitivity analyses. We varied the parameter *h,* representing predator efficiency or hunger level (Eq. 3; Andersen 2019), to change the allometric properties of the risk of predation (Supp. Fig. 6). However, while varying this parameter affected the realized lifespans, it did not dramatically change individual growth trajectories or patterns of size-specific reproduction (Supp. Fig. 6). By contrast, the constraint on the amount of lipid stores that can be spent each month on reproduction, φ, was of more importance for growth because it depended directly on the individual's structural mass. This parameter contributes biological realism to the state dynamics, but is difficult to measure or estimate directly, especially for fish that spawn multiple times per year, because often little is known about the frequency of spawning. In sensitivity analyses, we found that making this constraint more stringent (e.g., decreasing φ from 0.2 to 0.1) led to increased body sizes, and this pattern held at both high and low productivity values (Supp. Fig. 7). Finally, we used estimates of parameters for the metabolic cost function that were measured experimentally for tuna species, because of our interest in explaining diversity in tuna growth patterns (Clarke and Johnston 1999). However, to understand if the relatively small effect of increased temperatures on body size in Figure 5 was robust to differences in physiological costs, we conducted sensitivity analyses in which the shape and allometric scaling of costs varied (Supp. Figs. 8 and 9). We confirmed that our choice of parameters for this function had relatively minor influences on growth and reproduction.

In the environmental scenarios representing the three ecological lifestyles of tunas (Table 2) our model predicted growth, body size, and reproductive patterns that are representative of typical species of each of the three tuna ecological lifestyles (Figure 6). With the environmental scenario representing the tropical shallow-diving lifestyle, we predicted a maximum body size of 70 cm, longevity of 6-7 years of age, and continuous reproduction at relatively low levels (left column, Figure 6, Table 2). These predicted traits are similar to those of frigate tuna *Auxis thazard,* a tropical shallow-diving tuna species with small body size. With the environmental scenario matching the tropical deep-diving lifestyle, we predicted growth to sizes well over 200 cm, lifespans of less than 15 years, and continuous reproductive output that increases over the individual's life (middle column, Figure 6, Table 2). While we believe this is broadly consistent

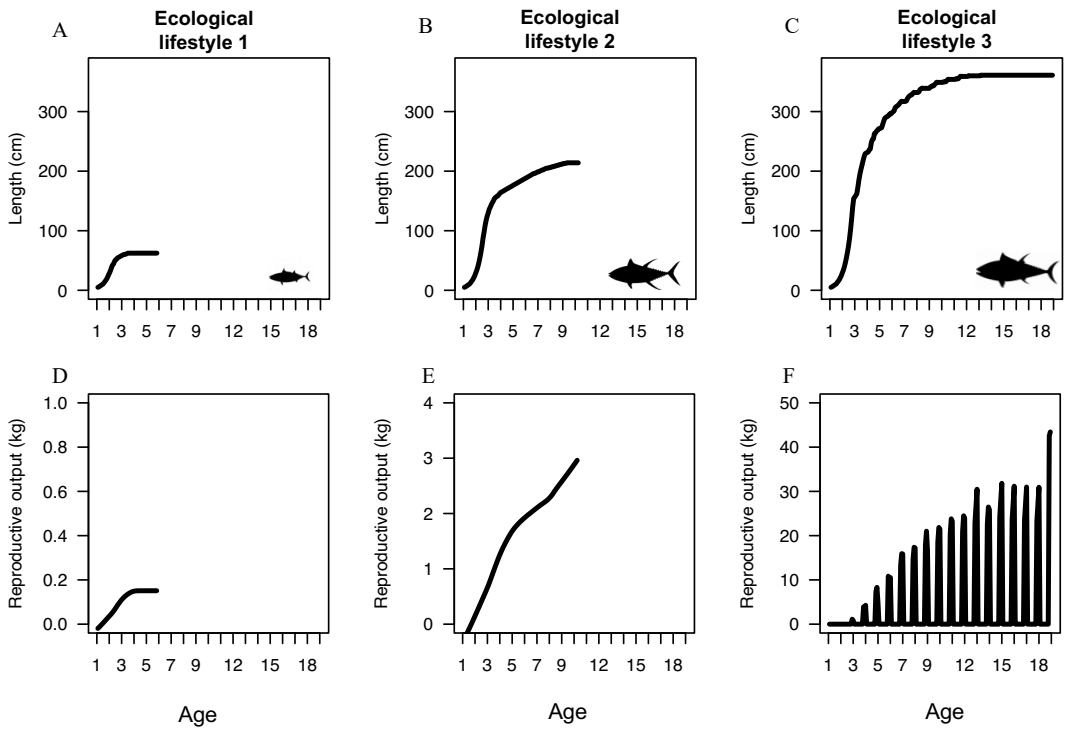

Figure 6. Growth (top row) and reproduction (bottom row) predicted by our general energy-based model for the three characteristic ecological lifestyles of tunas using three representative environmental scenarios (columns). Details of each scenario and species are in Table 2. With the exception of C and F, all curves end at the age when less than 3% of the population is expected to survive, representing the cohort lifespan. A and D represent tropical shallow-diving tuna species such as the frigate tuna *Auxis thazard*. B and E represent tropical deep-diving tuna species such as yellowfin tuna *Thunnus albacares*. C and F represent temperate deep-diving species such as Atlantic bluefin tuna *Thunnus thynnus*, which migrate seasonally from higher latitudes with colder and productive waters to less productive and warmer waters. At age 18, more than 10% of individuals in the temperate deep-diving lifestyle were still alive and are likely to live much longer (C, F). As in Fig. 4, the reproductive output in panels D-E was smoothed using the loess function.

530 t

531 with the life histories of tropical deep-diving tuna species such as yellowfin tuna *Thunnus*

532 *albacares*, lifetime reproductive patterns of these batch-spawning species are not well known

(Horswill et al. 2019). In the environmental scenario matching the lifestyle of temperate deep-diving tunas, such as Atlantic bluefin tuna, *Thunnus thunnus,* we predicted the maximum body size exceeded 350 cm a longevity that was longer than 18 years (right column, Figure 6, Table 2). Spawning was constrained to be seasonal in tunas in the third ecological lifestyle (i.e., spawning could only occur in temperatures above 24 ℃, which we specified individuals experienced for three months of the year).

Analysis of seasonality in temperature and spectrum productivity

The results of the tuna case study yielded an unexpected pattern: when spawning activity, environmental temperature and ecosystem productivity varied seasonally, i.e., in the third ecological lifestyle of temperate deep-diving tunas, individuals grew to be substantially larger than the size observed under constant environment conditions that are otherwise comparable in terms of productivity (κ) and temperature (τ).

To investigate this pattern further, we made several follow-up comparisons of the effects of seasonality in spawning season length, temperature (in which species spawned for three months in waters that are 9 degrees warmer than their winter foraging grounds) and productivity (which increased threefold during the winter months spent on the foraging grounds). In Figure 7, for a range of ecosystem productivities ($\kappa = 0.5$ - 2.5 when averaged across the 12-month period), we compared the maximum lengths predicted in constant environments with scenarios in which reproductive season length varied (represented by the dash length in Fig 7), and/or temperature and productivity fluctuated over the year, for a total of 6 contrasting scenarios: (i) the most basic constant scenario when temperature, productivity (κ), and spawning were constant year round

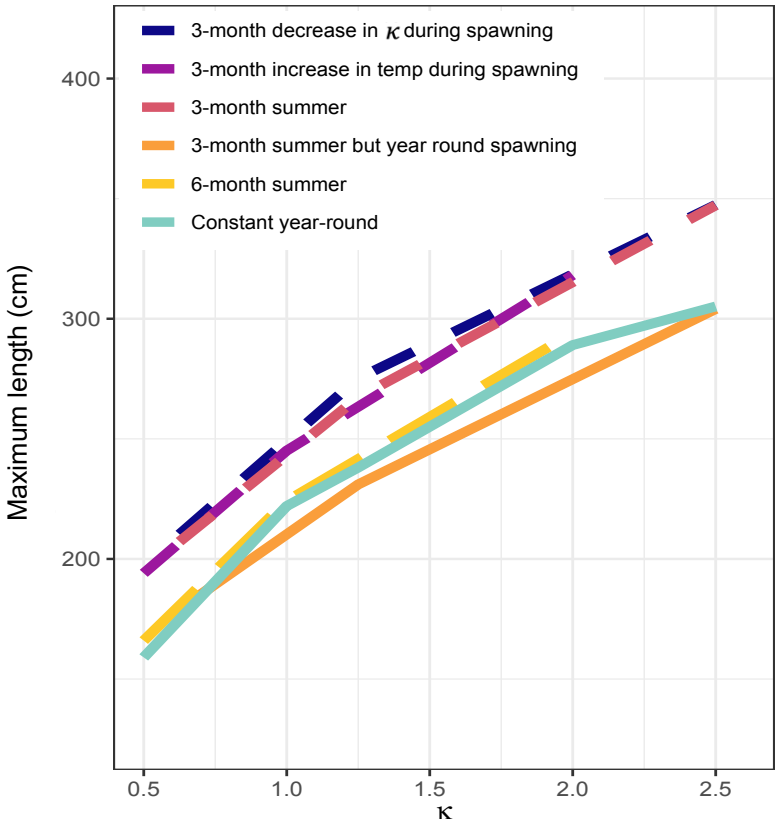

Figure 7. Maximum body length across values of κ in multiple scenarios varying seasonality in food, temperature, and spawning season duration. As described in the text, solid lines represent scenarios where spawning is possible every month of the year, while the dashed lines represent scenarios where spawning is restricted to three months (short-dashed) and six months (yellow long-dashed) of the year. Colors correspond to different scenarios in which temperature and productivity fluctuate temporally.

(solid aqua line in Figure 7, which is identical to the τ = 16.85 °C scenarios shown in Fig. 5); (ii) a seasonal scenario when temperature increased during the three month spawning season but productivity κ did not change throughout the year (purple short-dashed line in Fig. 7), (iii) a seasonal scenario with a threefold increase in productivity for nine months to represent time

spent in foraging grounds, but with temperature kept constant throughout the year (navy blue short-dashed line in Fig. 7); (iv) the full seasonal scenario where productivity and temperature varied during the three-month summer when spawning was possible (salmon pink short-dashed line in Fig 7; note this scenario is similar to Fig. 6C, but with lower values of κ); (v) a full seasonal scenario where the warm, low-productivity season lasted for six months instead of three (yellow long-dashed line in Fig. 7); and (vi) a seasonal scenario where productivity and temperature varied during the three-month summer but spawning was possible during the full twelve months (solid orange line in Fig. 7).

These comparisons clarified that the restriction of spawning to three months of the year has the largest effect on maximum body size across a range of ecosystem productivities (because the short-dashed lines are substantially greater than solid or long-dashed lines in Fig 7). When spawning was restricted to three months, the effects of temperature and productivity alone were comparable to those when both effects are combined (in Fig. 7, the three short-dashed lines are similar). When spawning was restricted to 6 months of the year, and temperature and productivity fluctuated seasonally, individuals grew to intermediate sizes. Smaller sizes were predicted when spawning was possible during every month of the year, especially when temperature and productivity fluctuated seasonally (the solid orange line in Fig. 7). From this set of follow-up analyses, we inferred that resources and temperature effects on energetic budgets were not the primary drivers of larger body sizes in our model. Rather, the compression of reproductive opportunities into three months of the year, and the temporal separation of reproduction from the most valuable foraging opportunities, favors increased allocation to growth.

Discussion

We modeled the evolution of growth and reproduction in fish in differing environments, accounting for food web interactions represented by size spectra, and the effects of seasonality in metabolic demands and spawning opportunities. With our general energetic model we also were also able to predict observed life history traits of species representing the three main ecological lifestyles of tunas. By unpacking the effects of temporal variation in spawning opportunities, metabolic demands, and foraging opportunities, we predicted that seasonal cycles in resource intake and expenditures have a greater effect on the evolution of body size than that of temperature on metabolic rate.

Changes in environmental temperature and ecosystem productivity have been occurring for decades and have been shown to affect fish recruitment, growth, and fishery productivity (Free et al. 2019; Oke et al. 2020). There have been several mechanisms proposed to explain these changes (Fernandes et al. 2020). Early models based on differences in resource intake and metabolic demands predicted that increased temperature will lead to reduced growth and smaller body sizes, i.e., 'shrinking fishes' (Cheung et al. 2008), but experimental evidence shows growth is less affected by temperature than reproductive allocation (Wootton et al. 2022), and that metabolic rate can adapt to increased temperatures (Pilakouta et al. 2020). Critically, such physiological models and experimental observations necessarily minimize confounding effects of environmental productivity, seasonality, and ecological interactions. Our model is fundamentally different, as we incorporated all these extrinsic abiotic and ecological factors that previous work has had to ignore. Our general energetic model used insights from size-sspectrum theory to parametrize the availability of prey (foodscape) and the risk of predation (fearscape) for

individuals of different sizes into a model of individual fitness. The minor effect of temperature on our model results implies that temperature is relatively unimportant compared to foraging and surviving in the real world.

A key difference between our general energetic model and other models of life history evolution of fishes in different environmental conditions is that we consider the mass-specific scaling of metabolic costs with temperature in addition to differences in primary productivity, which drives food-web interactions. Across a range of temperatures, our model predicted the benefits of growing large through the foodscape and fearscape outweighed the increase in metabolic costs until very large sizes and/or very dramatic increases in temperature. For example, although our model predicted smaller body sizes and decreased lifetime reproduction at higher temperatures when both predators and prey were scarce, these differences were relatively small until average temperatures increased by 10-15 ℃. Ecosystem productivity κ had a much stronger influence on our results than any of our other parameters; consistent with expectations, our model predicted larger maximum body sizes, greater reproductive output, and longer lifespans in more productive ecosystems. One exception came when estimating age-specific mortality of each environment, which was more sensitive to our choice of the value representing variation due to predator satiation or efficiency in prey capture (*h,* Eq. 3). However, this process did not substantially change growth trajectories.

Our results provide a novel explanation for asymptotic growth, which does not invoke metabolic mechanisms or trade-offs between growth and reproduction. Prior work has explained asymptotic growth patterns with physiological arguments for intrinsic geometric constraints (von

629 Bertalanffy 1960, Pauly 2010), or by specifying that increased allocation to reproduction limits
630 allocation to growth, leading to a slowdown in growth rate with age (Jusup et al. 2011). In our
631 model, multiple (mainly extrinsic) ecological mechanisms led to slowing of growth and
632 emergence of an asymptotic size in each environment. Unlike previous research, in our model
633 the onset of reproduction alone does not correspond immediately to decreasing growth. Instead,
634 the availability of prey, the physical and temporal limits on resource intake, the risk of predation,
635 and constraints on gonad size and reproductive timing all increase the advantage of growing to
636 larger body sizes; these advantages are balanced against metabolic demands and the actual
637 energetic requirements of growth.
638
639 We used variation among the ecological lifestyles of tunas as a motivation for our model
640 parameterizations and comparisons, while also aiming to provide general insights into the
641 evolution of fish life histories. We successfully predicted growth and reproductive patterns that
642 are consistent with species representing each ecological lifestyle of tunas (Fig. 6). Unexpectedly,
643 we found an effect of seasonal variation on body size. Further investigation revealed this effect is
644 robust to fluctuations in temperature or in productivity alone, and is largely determined by the
645 spawning season duration. These findings rule out explanations for spatial gradients in body size
646 based on metabolic costs, and strongly supports the conclusion that growth is driven by the
647 limited time available for reproduction, coupled with the opportunity to forage and store energy
648 in productive ecosystems the rest of the year. These results could explain giantism of fishes in
649 highly seasonal polar environments. For fishes like tunas, which often exhibit a combination of
650 capital and income breeding, and for which reproduction is determined by temperature, we
651 expect that as climate change generates warmer conditions, it will eventually allow spawning at

higher latitudes for longer periods. Yet our results suggest that cascading effects on their growth are not easily predicted and will depend on how warming waters reverberate through the size spectrum.

Our model illustrates that predicting responses in growth and reproduction in changing environments is complex, because optimal strategies responding to selective pressures from many factors, including intrinsic constraints on storage and reproduction, physiology, and the nature of ecosystem fearscapes and foodscapes. We have made several simplifying assumptions that could be explored in further investigations. For example, in the analyses presented here, we have assumed a static relationship between length and mass, and the conversion of mass to joules (energy density of tissue). Keeping these relationships constant ensured a common currency linking individual energetic budgets to ecological changes in predation risk and foraging success. Exploring the consequences of these relationships for differences among clades would be a natural follow-up to our study. Furthermore, while we did not directly address the interaction between of fisheries induced selection and growth, it is a rich area of further investigation (Audzijonyte et al. 2016). Plastic or evolutionary responses to fishing potentially include faster growth, earlier maturation rates, and smaller maximum body sizes, but the consequences for marine food webs are complex (Hočevar and & Kuparinen 2021). The framework introduced here potentially could capture how eco-evolutionary feedbacks between fishing mortality, growth and mass relationships, and ecosystem size spectra interactively affect trends in body sizes of focal species. Studies of the interaction between fishing and size spectra have been focused on lake systems where food webs have been studied in greater detail (Perälä and Kuparinen 2020). Understanding how these physiological and ecological processes are

mechanistically linked is necessary to understand how species will respond to different environmental changes and climate change scenarios in the ocean.

In summary, our findings suggest that when predicting future growth patterns under projected changes in climate, ecological and physiological factors - primary production, prey size and availability, and predation risk - will all play a greater role than temperature in determining trends in body size. We appreciate that our conclusion that increasing model complexity reveals a limited effect of temperature on growth may be unpopular. Nevertheless, we offer our model as a step toward models of fish growth with higher fidelity to nature that incorporate not only physiology and energetic allocation budgets but are also embedded in mass-specific foodscapes and fearscapes represented by size spectra. We hope that further exploration of our approach may lead to reconciliation of divergent results regarding the effect of climate change on fish body sizes.

Appendix. Optimization details.

Dynamic programming equations (Eq. 12) are constrained optimization algorithms with the purpose of determining the optimal set of behaviors or decisions that maximize a quantitative metric over time, such as lifetime expected reproductive success. A key property is that the decisions at one time affect the state variables at the next time. When solving Eq. 12, we consider how the allocation decisions an individual makes during one month of its life affect its future size, energetic reserves (lipid stores) and chances of survival, and find the set of allocation to growth and reproduction that maximizes its fitness in a given environment. We are able to calculate lifetime fitness by solving the equation using backwards iteration. By starting at $t =$

$T - 1$, and assuming there is no possibility of future fitness (i.e., the second term of Eq. 12 is equal to zero for all possible values of length and lipid stores) we can populate the array with the fitness of all possible combinations of length, lipid stores, and allocation strategies at $t = T - 1$; this fitness will be the first term on the right side of Eq. 12. This process is repeated, working backwards, until $t = 1$. We can thereby determine the combination of g and r that maximizes both current fitness at t, and the fitness expected from $t + 1$ until T, given the chance of survival, length, and lipid stores resulting from that particular strategy. Solving Eq. 12 in this way produces an array storing the proportional allocation to growth and reproduction that leads to the highest lifetime fitness, for all possible combinations of size and lipid stores (l and s) for every month until the final time T.

Solving a dynamic programming equation with two state variables, such as Eq. 12, is computationally expensive, and we employed a number of techniques to make the iteration more efficient and to approximate a smooth fitness surface. First, we constrained the parameter space that was evaluated. Specifically, we used an integer index I (with a maximum of I_{max}) to represent lipid stores s, converting the index to values in joules in the dynamic loop. We then related the range of s we explored to each value of l (because lipid stores are constrained by l), by setting

$$s = \frac{0.6 \cdot I^3 \rho a {l_{max}}^3}{{I_{max}}^3}$$

In other words, we adjusted the numerical step size for possible values of s to be finer for smaller individuals. Furthermore, we used linear interpolation of state values (Clark and Mangel 2000) when computing expected future fitness in Eq. 12 to minimize discontinuities on the fitness landscape arising from the integer index of energetic state. We did not interpolate length, since

its unit (centimeters) was sufficiently fine-grained that there were minimal effects of discontinuities.

We found that sharp transitions in the fitness landscape, such as at threshold values representing constraints, hindered our optimization algorithm. Therefore, we used an asymptotic function for the fitness increment associated with a given level of reproductive output. We let $R(r, s, l, t)$ denote the potential increment in fitness in month *t* when $L(t) = l$, $S(t) = s$, and a fraction of stores *r* is allocated to current reproduction, and assumed that R increased smoothly toward the maximum possible for the given length *l:*

$$R(r, s, l) = \frac{rs}{1+({rs}/{\varphi w(l)})f}$$

The asymptotic value of this function depends on the value of *f* in the denominator, which controls the abruptness of the constraint on current fitness (Supp. Fig. 2). In other words, the steepness of the multivariate landscape around the fitness optimum is modulated by *f.* For simplicity, we assume $f = 1$ for all results presented hereafter. In that case, when $\varphi w(l) >> \frac{rs}{\rho}$, $R(r, s, l) \sim rs$ and when $rs >> \varphi w(l)$, then $R(r, s, l) \sim \varphi w(l)$.

All programming was done using R 4.1.1. We ran the code to solve the dynamic programming equation and simulate the individual life histories using Rscript commands from the Linux shell of a 2019 MacPro with 16 cores and 96 GB of RAM. Jobs were run in parallel and the runtime of each job was between 60 and 120 minutes. The results of each job are presented in the figures summarizing growth, reproduction, and survival data; these analyses and figures were produced in the Rstudio IDE.

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1055 **Table 1**. Description of parameters and variables

Parameter or Variable	Description	Value
w	Body mass in kg	-
N	Number of individuals in a size category (or trophic level) when considering a Sheldon size spectrum	-
B	Absolute biomass in a size category (or trophic level) when considering a Sheldon size spectrum	-
κ	The spectrum parameter, which defines the total biomass of organisms of the smallest body size w in a given ecosystem; Andersen (2019) gives an estimate of 10 gained by averaging over all Predator-Prey Mass Ratio estimates measured from gut contents. We vary it to represent ecosystem differences in overall ecosystem productivity	Varies
$Bprey$	Biomass of prey expected by a focal individual	-
μ_p	Instantaneous risk of mortality due to predation, which depends on body mass and position in the size spectrum	-
h	Predation risk, comprised of predator satiation estimates (estimated from gut contents) and predator preference (or effectiveness) for consuming prey of a given mass (Andersen 2019)	4, 8
τ	Temperature of the environment (in degrees Kelvin except where noted)	285-300
C	Metabolic requirements (costs) that scale with mass and temperature	-
c	Normalization constant scaling metabolic costs (in J), based on metabolic rate data from tunas (Kitchell et al. 1978)	5×10^{16}
k_B	Boltzmann constant, relating particle energy to temperature in units of m^2 kg s^{-2} K^{-1}	1.3×10^{-23}
E	The average activation energy for the rate limiting enzymes in metabolism in units of joules; from the metabolic theory of ecology (Gillooly et al. 2001).	1.04×10^{-19}
θ	Metabolic scaling exponent; values vary among clade, here we use a value reported for tunas (Clarke and Johnston 1999)	0.66
ρ	The energy density of tuna body mass in our model in J/kg (estimated empirically and reported in Chapman et al. 2011)	4.2×10^{6}
t	Time in monthly time steps in the dynamic model	-
T_{max}	Maximum lifespan in months	216
l, $L(t)$	Body length (in cm) This is a dynamic state variable but can only increase with time. The maximum value possible is 400 cm. For a specific value, we use the capital letter notation.	-
s, $S(t)$	Lipid stores (in joules) – this is a dynamic state variable representing energy stores that can be used for metabolism, growth, and reproduction.	-
a	Scale coefficient relating length to structural mass, similar to values estimated empirically for bluefin tuna and reported in Pignalosa et al. (2020).	1.0×10^{-5}
$w(t)$	Structural mass of the individual (in kg) at time t – this depends on $L(t)$	-
υ	The fraction of structural mass that determines the critical threshold of energetic mass needed for survival	0.1
φ	The fraction of structural mass that determines the maximum possible reproductive output in a monthly time step	0.2
γ_{pred}	Survival from predation from one month to the next	
γ_s	Survival, given that the individual has sufficient energy reserves to meet metabolic requirements and avoid starvation	
g	Proportion of lipid stores allocated to growth (this allocation decision is optimized by the dynamic programming equation); can take values between 0 and 1	
r	Proportion of lipid stores allocated to reproduction (this allocation decision is optimized by the dynamic programming equation); can take values between 0 and 1 and the sum of g and r cannot exceed one.	
$R(l,s,t)$	Current fitness, the product of lipid stores and the optimal allocation to reproduction, r	
$V(l,s,t)$	Expected accumulated lifetime reproduction from time t onwards, given that $L(t) = l$ and $S(t) = s$	

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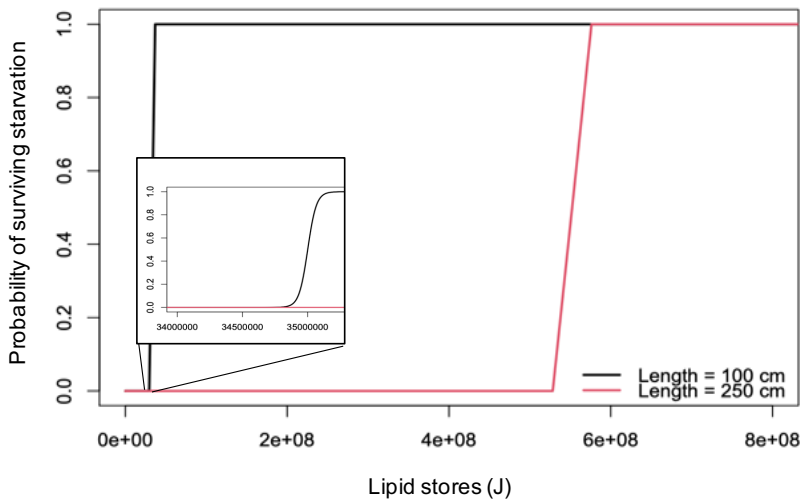
Table 2

Parameter values for environmental scenarios corresponding to the three ecological lifestyles of tunas described in Fig. 3, with corresponding predicted body size and maximum observed fork length (cm) for three representative species (data from Juan-Jordá et al. 2016).

Lifestyle	**Environment**	**Baseline or winter temp**	**Yearly mean κ**	***h***	**Predicted body size**	**Representative species**	**Reported range of body sizes**
Tropical shallow	Constant	26.85 C	0.1	8	62 cm	Frigate tuna	40-60 cm
Tropical deep diving	Constant	21.85 C	1	8	214 cm	Yellowfin tuna	125-231 cm
Temperate deep diving	Seasonal	11.85	2.5	12	361 cm	Bluefin tuna	203-427 cm

Supplemental Table 1. Model outputs corresponding to points in main text Figure 5. All scenarios had constant environments.

Temperature τ in ℃	κ	Lifetime reproductive output (kg)	Maximum body length (cm)
11.85	0.25	2.15	109.5
11.85	0.5	5.87	173
11.85	1	15.51	224
11.85	2	38.94	289.1
11.85	5	123.77	390.4
16.85	0.25	2.08	101.5
16.85	0.5	5.9	159
16.85	1	15.2	222
16.85	2	37.97	289
16.85	5	121.95	384.3
21.85	0.25	2.02	98.4
21.85	0.5	5.65	159
21.85	1	14.73	214
21.85	2	36.93	282
21.85	5	119.28	380.3
26.85	0.25	1.85	92.4
26.85	0.5	5.33	151
26.85	1	13.85	202
26.85	2	35.15	274
26.85	5	115.73	373.4



Supplementary Figure 1. Main panel: The sigmoid relationship between lipid stores (in joules) and survival for individuals of different lengths. The threshold amount of energy required for metabolic maintenance is a fixed proportion of body mass. The probability of avoiding starvation $\gamma_s(s, l)$ is a logistic function of mass given in Eq. 11. Inset: closeup of the x-axis in the region encompassing the smaller threshold.

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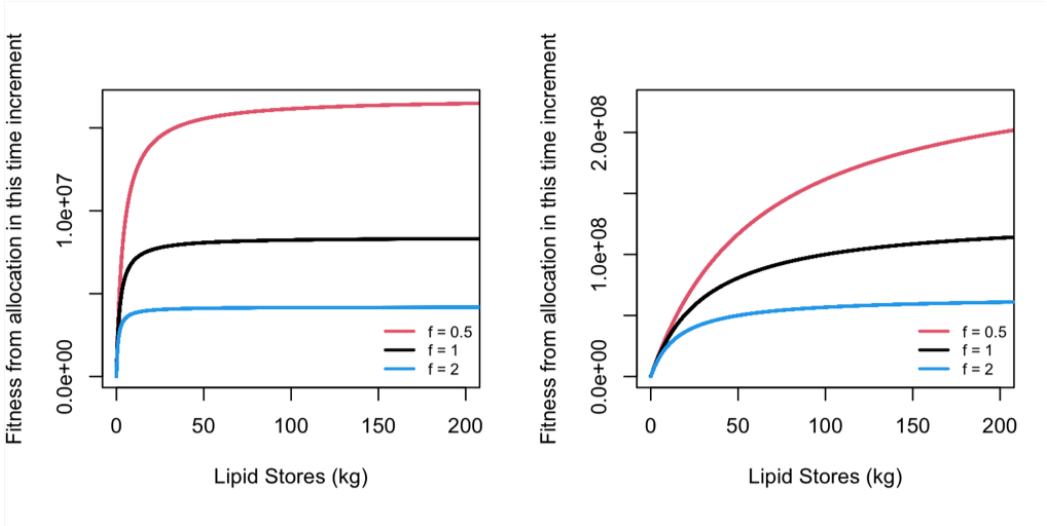
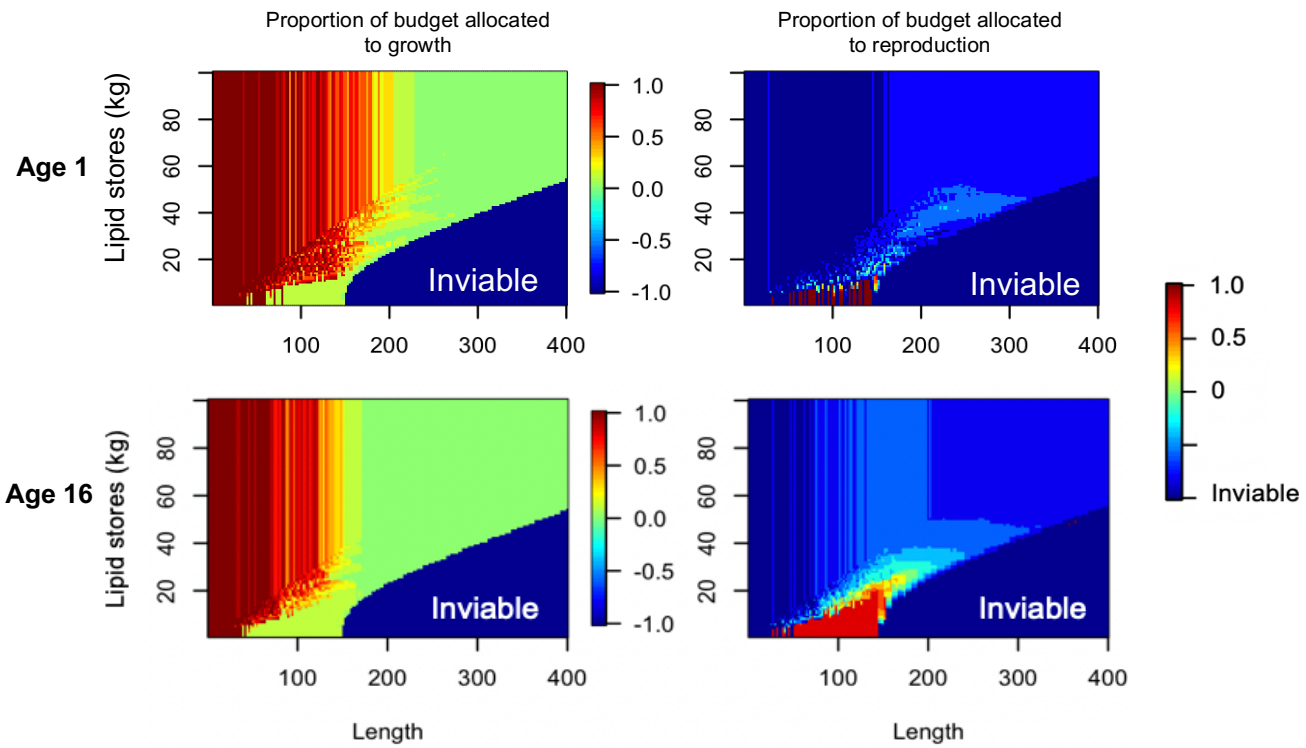
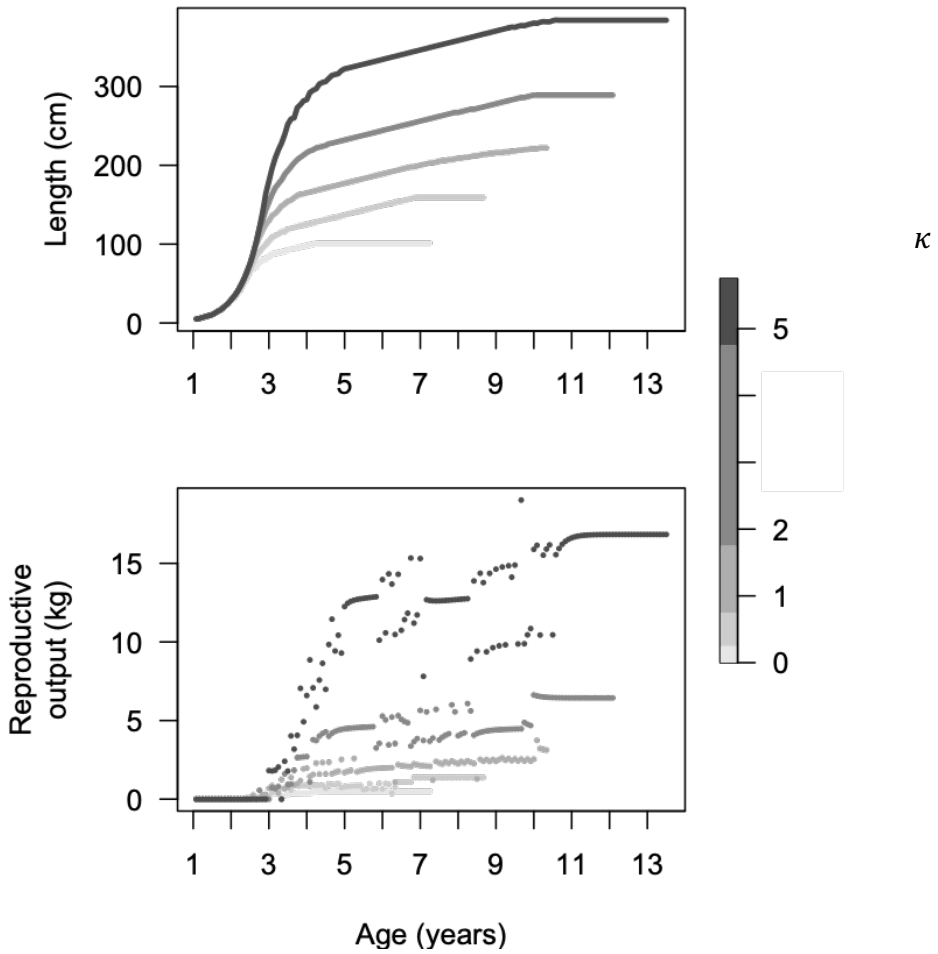


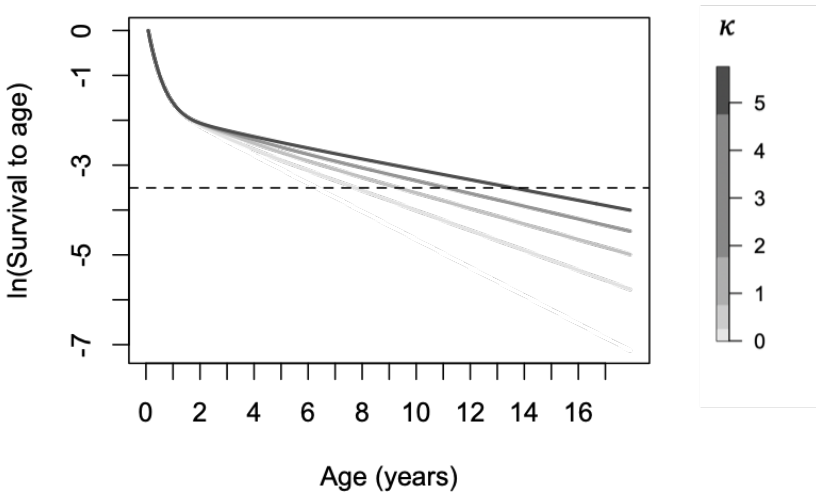
Supplementary Figure 2. The fitness increment expected with different amounts of lipid reserves (energy stores) Left panel: Fitness increment for an individual of 100 cm. Right panel: Fitness increment for an individual of 250 cm. We show the shape of the function for three values of *f* but for all analyses here we used *f* = 1.



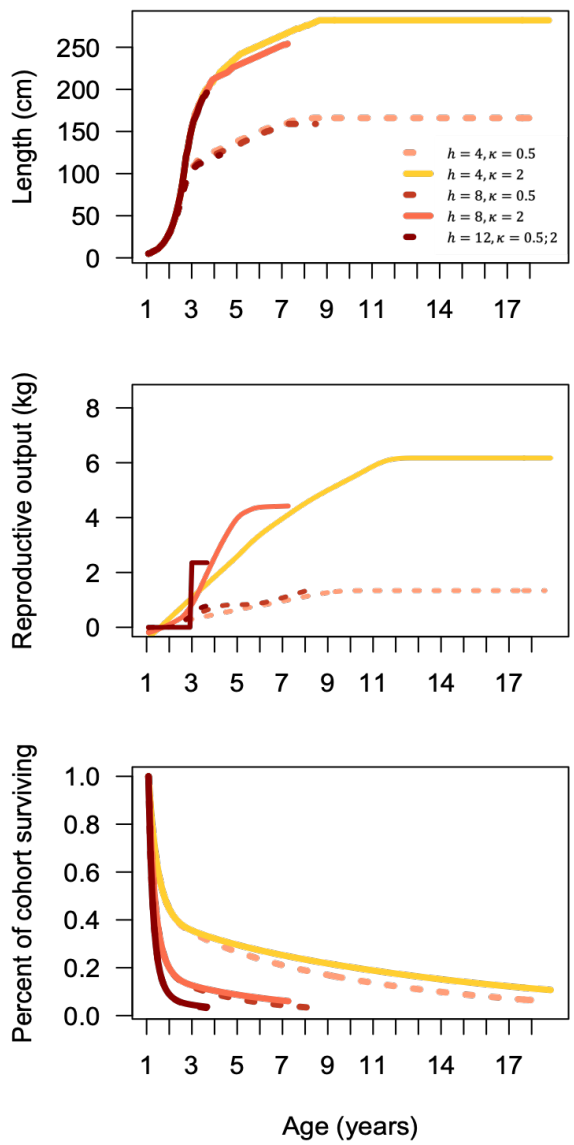
Supplementary Figure 3. Example rules for allocation to growth and reproduction for ages 1 and 16. The inviable region (dark blue) represents parameter space where remaining stores are insufficient for survival, given the individual's length (in other words, energetic requirements for maintenance are not met). Comparing panels within rows shows differences between allocation to growth and reproduction as a function of state and length. Comparing panels within columns shows how the tradeoff between growth and reproduction changes with age. Note that the striations come from the discretization of allocation values of g and r in Eq. 12.



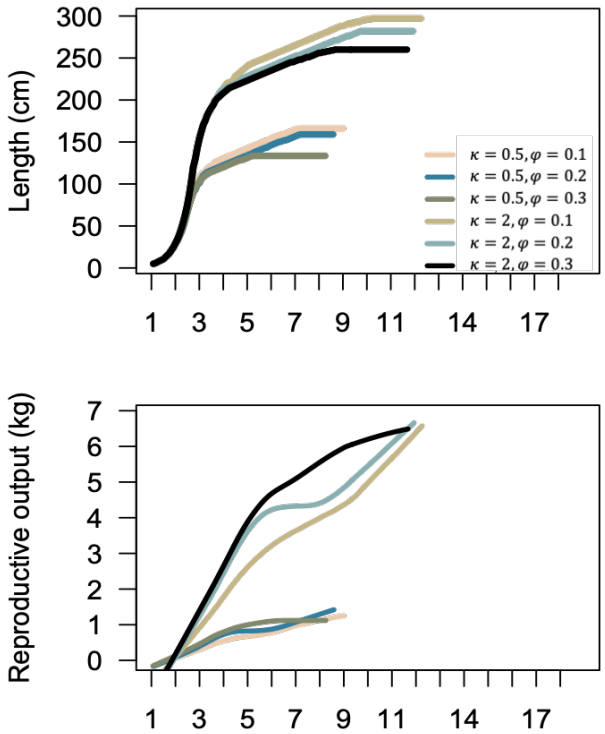
Supplementary Figure 4. Top: The emergent pattern of survival to age at different levels of κ. Bottom: The natural log of survival to age. Dashed horizonal line shows the cutoff past which less than 3% of individuals will survive. For all results here, $h = 8$ and $\tau = 16.85$℃



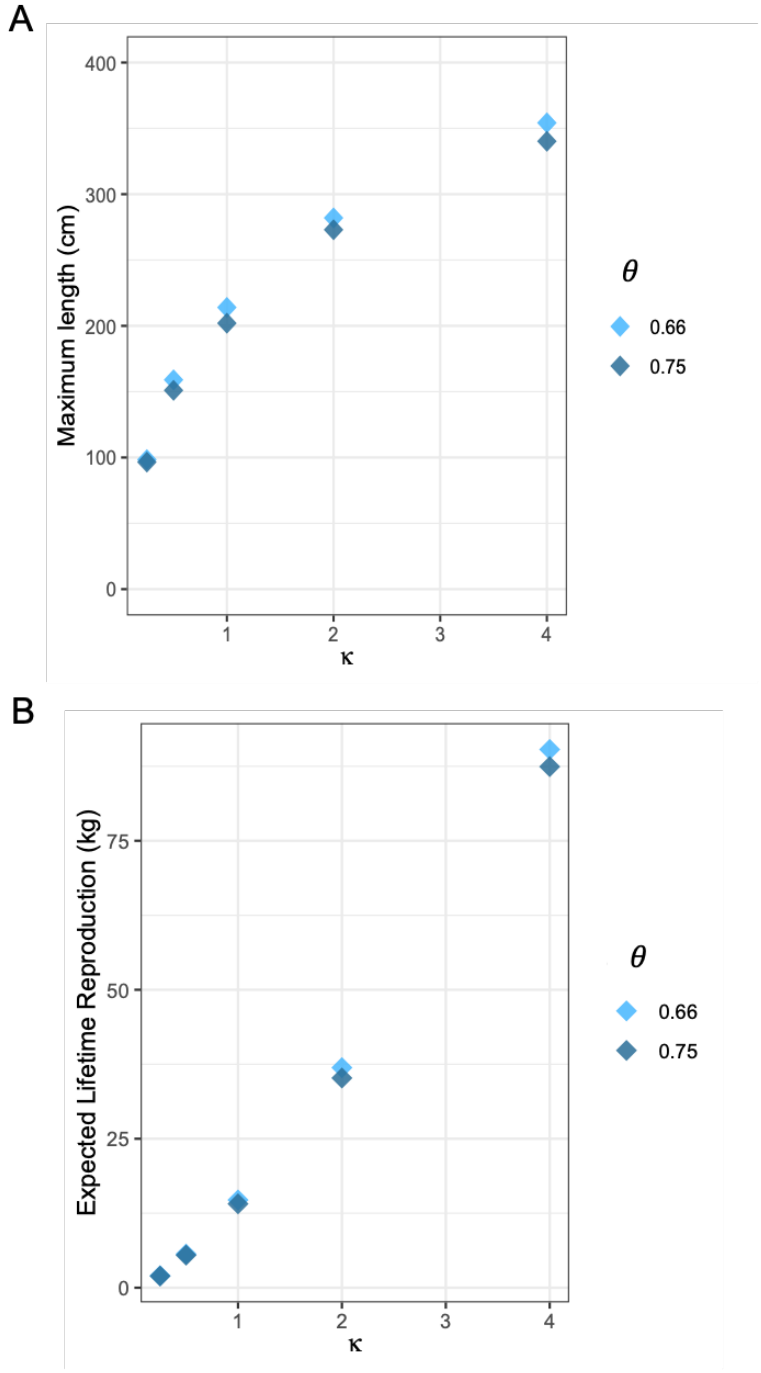
Supplementary Figure 5. The emergent pattern of ln(survival) to age at different levels of κ. Dashed horizonal line shows the cutoff past which less than 3% of individuals will survive. For all results here, $h = 8$ and $\tau = 16.85$℃.



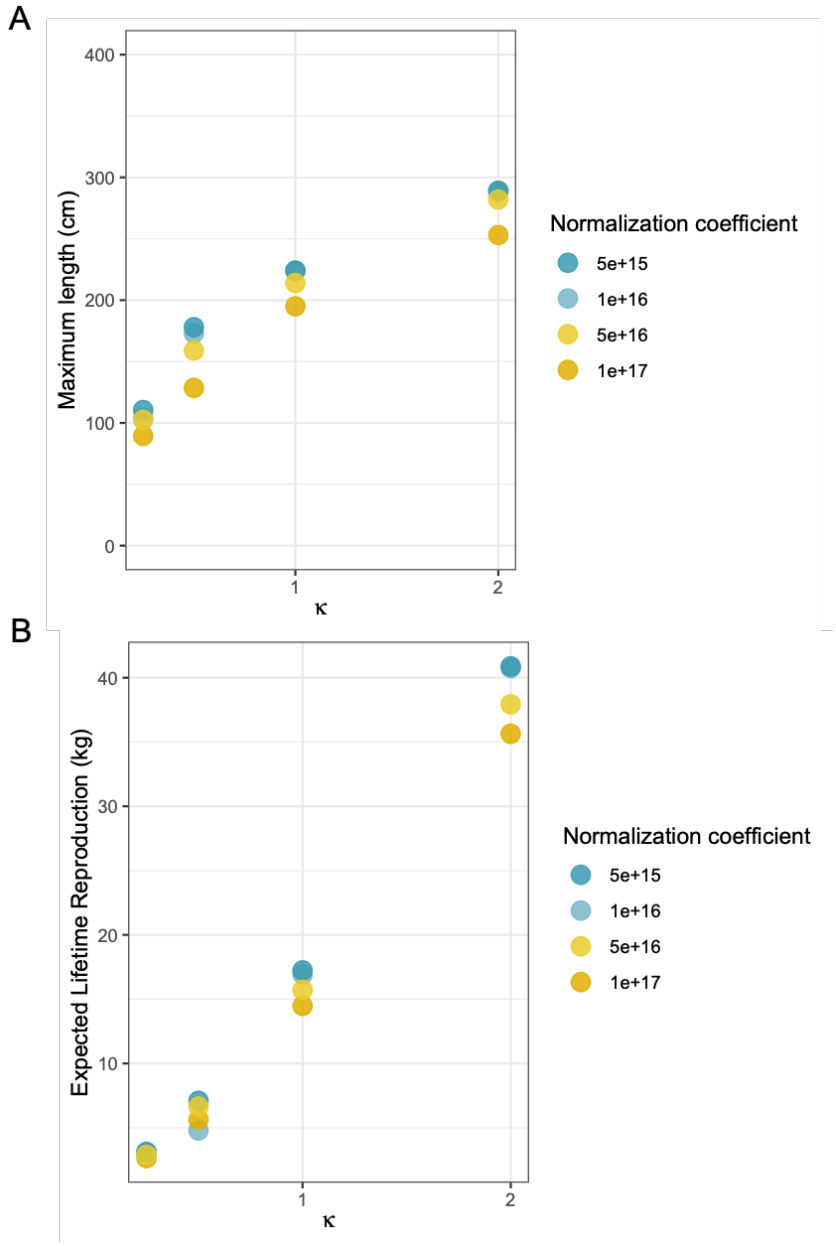
Supplementary Figure 6. The emergent patterns of growth, reproduction, and survival that emerge when h varies. We contrast two values of κ to highlight that it is still the main driver of variation in body size, although h affects lifespan. In all scenarios, $\tau = 16.85°C$. Note that for results presented elsewhere, $h = 8$ except where noted.



Supplementary Figure 7. Growth curves showing the effect of changes in the reproductive capacity φ, for two values of κ. As the reproductive constraint increases (the fraction of the body cavity that can be devoted to gonad decreases from 0.2 to 0.1), selection favors the evolution of larger body sizes. In all scenarios, $\tau = 16.85$℃. Note that for all results presented elsewhere, $\varphi = 0.2$.



Supplementary Figure 8. Body size and lifetime reproduction for several values of κ and θ (the allometric exponent in the metabolic cost function). For all scenarios, temperature is constant year-round at 21.85°C.



Supplementary Figure 9. Body size and lifetime reproduction for several values of κ and c (the normalization constant in the metabolic cost function). The estimate of c used elsewhere (5×10^{16}) comes from metabolic rate data from tunas (Clarke and Johnston 1999). For all scenarios, temperature is constant year-round at 21.85°C.